

Greater Focus Needed on Alien Plant Impacts in Protected Areas

Philip E. Hulme¹, Petr Pyšek^{2,3,4}, Jan Pergl², Vojtěch Jarošík^{2,3,*}, Urs Schaffner⁵, & Montserrat Vilà⁶

¹ The Bio-Protection Research Centre, Lincoln University, Canterbury, New Zealand

² Institute of Botany, Department of Invasion Ecology, Academy of Sciences of the Czech Republic, Průhonice, Czech Republic

³ Department of Ecology, Faculty of Science, Charles University in Prague, Prague, Czech Republic

⁴ Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland 7602, South Africa

⁵ CABI, Delémont, Switzerland

⁶ Estación Biológica de Doñana (EBD-CSIC), Sevilla, Spain

Keywords

Biological invasions; community structure; exotic species; fire; macroecology; national parks; nature reserves; plant conservation; soil processes; weeds.

Correspondence

Philip E. Hulme, The Bio-Protection Research Centre, PO Box 84, Lincoln University, Christchurch, New Zealand.

Tel: +64 3 321 8317; fax: +64 3 325 3864.

E-mail: Philip.Hulme@lincoln.ac.nz

Received

6 May 2013

Accepted

13 August 2013

*Deceased.

Editor

Julie Lockwood

doi: 10.1111/conn.12061

Abstract

Alien plants pose significant threats to protected areas worldwide yet many studies only describe the degree to which these areas have become invaded. Research must move toward a better understanding of alien plant impacts since managers urgently require an appropriate evidence base to prioritize control/eradication targets. We analyze a global database of quantitative studies of alien plant impacts to evaluate existing knowledge of alien plant impacts within and outside protected areas. Although protected areas are a significant focus for quantitative impact studies, the biogeographic emphasis of most research effort does not coincide with the global distribution of protected areas nor the plant species or life-forms recognized to have greatest impacts on ecosystems. While impacts were often as significant within protected areas as outside, only a minority of studies provide any subsequent management recommendations. There is therefore considerable scope to improve the evidence base on alien plant management in protected areas.

Introduction

Protected areas provide the core of efforts to safeguard the world's threatened species and represent the fundamental building blocks of most national and international conservation strategies (Dudley 2008). Yet, many protected areas face major threats arising from both illegal (e.g., encroachment, logging) as well as officially sanctioned (e.g., mineral/petrochemical extraction and road/rail infrastructure) activities (Laurance 2013; Leroux & Kerr 2013). In addition to, and often in association with these threats, the problems caused by the ingress into protected areas of invasive species, and particularly alien plants, represent a further challenge (Loope *et al.* 1988; Macdonald & Frame 1988; Macdonald *et al.* 1988). Increasingly, the success of protected areas to achieve the

long-term conservation of nature will reflect the interaction of these multiple pressures on biodiversity (Sodhi *et al.* 2010). Yet, in contrast to many other pressures (Bruner *et al.* 2001; Andam *et al.* 2008), there is a shortage of consolidated information at global and/or regional levels on alien species impacts in protected areas (GISP 2007).

Current understanding of plant invasions in protected areas has largely focused on the degree to which these areas have become invaded. The number of alien species is often positively correlated with native species richness of the protected area (Pyšek *et al.* 2002; Allen *et al.* 2009) but protected areas tend to harbor as few as half as many alien plants species compared to surrounding areas (Lonsdale 1999; Pyšek *et al.* 2002). These two trends suggest that the vulnerability of protected areas to invasion may

be less a function of biotic resistance but better reflect the magnitude in propagule pressure (but see Pyšek *et al.* 2003). This is supported by the finding that alien plant richness is often a strong positive correlate of the number of visitors to protected areas (Usher 1988; Lonsdale 1999; Allen *et al.* 2009) and these visitors are recognized as important vectors of alien plants (Pickering & Mount 2010; Hulme *et al.* 2012). Evidence that the perimeter to area ratio of protected areas and their proximity to human settlements are also associated with the richness of their alien floras provides further support for an important role of propagule pressure in the observed levels of invasion (Timmins & Williams 1991). Thus, recent progressive human encroachment at protected area boundaries (Radeloff *et al.* 2010; Leroux & Kerr 2013) should be especially worrying since it will augment alien plant propagule supply as well as facilitate visitor access resulting in further invasions (Rose & Hermanutz 2004; Spear *et al.* 2013).

Given that alien plant species are impervious to legislative boundaries, the foregoing paints a rather stark future for protected areas. In this respect, research has to move from describing patterns of alien plant species richness toward a better understanding of alien plant impacts in protected areas. For example, as yet there has been no assessment of whether alien plant impacts differ in their magnitude within and outside protected areas. Furthermore, since only a minority of alien plants in protected areas are likely to pose a threat to biodiversity (Groves 2002; Williams & Timmins 2002; Hulme 2012), managers urgently require an appropriate evidence base to prioritize control targets (Cook *et al.* 2010). Unfortunately, the evidence base to support effective and targeted management of alien plants in protected areas is often poor (Andreu *et al.* 2009). In contrast, there has been a rapid increase in quantitative studies assessing the magnitude of alien plant impacts on ecosystems (reviewed in Hulme *et al.* 2013). This raises the question as to the extent these studies might inform the management of protected areas. Here, we use an existing dataset of alien plant impacts in their invaded range (Vilà *et al.* 2011; Pyšek *et al.* 2012) to evaluate whether sufficient focus has been allocated to studies of impacts in protected areas. Specifically, we ask:

- (1) How well represented are impact studies within and outside protected areas and how does this vary across major biogeographical regions?
- (2) Do differences exist in the alien plant life-forms and/or types of impacts examined within and outside protected areas?
- (3) Are impacts generally more frequently significant within than outside protected areas?

The answers to these questions are used to assess the extent to which quantitative impact studies in protected areas might actually inform future management of alien plants and provide the basis for future recommendations.

Methods

We use a comprehensive database on quantitative studies of terrestrial alien vascular plant impacts that describe the frequencies of significant and nonsignificant impacts and their directions on a broad range of species and ecological attributes in both invaded (including experimental addition of alien species) and uninvaded (including experimental alien species removal) plots in natural or seminatural ecosystems (Pyšek *et al.* 2012; Hulme *et al.* 2013). A total of 25 impact responses were assessed that included: abundance, diversity, richness, biomass, fitness (e.g., fecundity), and performance (e.g., survivorship) of resident plant and animal species; animal and microbial activity; soil parameters such as organic matter content, nutrients (e.g., C, N, P pools and fluxes), minerals, pH, soil fauna and microbial richness and diversity; and plant tissue attributes such as litter decomposition rate; nutrient and mineral content and flammability. A systematic search of the peer-reviewed literature (described in Pyšek *et al.* 2012) resulted in a dataset that comprised 287 papers that addressed the impact of a particular alien plant species on one or more impact responses and statistically tested for significance between comparable invaded and uninvaded plots. To facilitate comparison across different impact responses, each case study was simply scored as to whether the observed impact was statistically significant ($P < 0.05$) or not. In total, 1,551 case studies (impact response \times location \times species) were examined across 167 taxa.

Using the site description in each publication, we scored each study in relation to whether it was undertaken in a protected area (e.g., national park, wilderness area, nature reserve, protected landscape, etc.) or not. This could be done unequivocally for most studies (282 publications) resulting in a final database of comprising 1,517 case studies of which 574 were undertaken within a protected area. While differences in land-use within and outside protected areas are often significant (Joppa & Pfaff 2011), the database only included studies of impacts in seminatural rather than anthropogenic ecosystems and this should facilitate the comparability of the data. To facilitate analysis and ensure adequate sample sizes, we aggregated the 25 impact responses into four major response classes: impacts on (i) populations, species, and communities of plants; (ii) populations, species, and communities of animals; (iii) soil attributes; and (iv) fire regime. We then compared the

frequency with which impacts were examined within and outside protected areas for these four response classes, eight biogeographic regions, and nine different plant life-forms. We also assessed whether the frequency with which a significant impact was found for each of the four response classes differed within and outside protected areas. For each of these analyses, differences between observed and average frequencies were tested by a *G*-test on the appropriate contingency tables. Finally, we examined the implications of these impact studies for management. First, we compared the representation of plant species recognized to be major environmental threats (listed by Weber 2003) in quantitative studies of impact within and outside protected areas. Second, we reviewed the studies undertaken in protected areas for any specific recommendations regarding the management of the focal alien species in the study region.

Results

Impacts have been frequently addressed in protected areas. Of a total of 282 published quantitative studies for which it was possible to infer the protection status of the study area, 37% were conducted in protected areas. Biases were found with regard to the geographical distribution of impact studies within and outside protected areas. In North and South America and on Pacific islands, disproportionately more impact studies have been conducted in protected areas than outside, while the opposite is true for Europe, Asia, and Africa ($\chi^2 = 239.85$; $df = 6$; $P < 0.001$; Figure 1A). There were considerable differences in the composition of species examined within and outside protected areas with only 31 (18.5%) having been studied in both. More than half of all species for which impacts have been examined quantitatively were only studied outside protected areas. Clear differences in the extent to which individual life-forms were examined within and outside protected areas were found ($\chi^2 = 232.85$; $df = 8$; $P < 0.001$; Figure 1B). There was a stronger representation of studies examining the impacts of biennial herbs, as well as annual and perennial grasses within than outside protected areas. However, this marked bias in life-forms also had a strong geographic bias. While studies in North America exhibited a strong bias toward examining the impacts of annual grasses in protected areas ($\chi^2 = 93.98$; $df = 8$; $P < 0.001$), this was not the case in the rest of the world where the main bias was toward perennial grasses and away from perennial herbs ($\chi^2 = 222.09$; $df = 8$; $P < 0.001$).

Differences were also apparent in relation to the type of impact examined inside and outside of protected areas. Overall, impacts of alien plants on soils were ad-

ressed in protected areas with a higher than average frequency, and on animals associated with invaded vegetation with lower frequency ($\chi^2 = 18.49$; $df = 3$; $P < 0.001$; Figure 2A). There were no major differences in the proportion of statistically significant impacts found within and outside protected areas ($\chi^2 = 1.86$; $df = 3$; $P = 0.61$; Figure 2B). The patterns strongly mirror those found for the frequency with which particular response classes were examined (Figure 2A) with fewer significant impacts reported within protected areas for populations, species, and communities of plants and animals. Although the impacts of a greater proportion of species listed by Weber (2003) were examined within (77.8%) than outside (64.2%) protected areas, the difference was only of borderline statistical significance ($\chi^2 = 3.59$; $df = 1$; $P = 0.058$). Of the 104 papers that describe studies within protected areas, only 33 (31.7%) contain explicit management recommendations regarding alien plant impacts. These recommendations most frequently address habitat restoration and the conservation of native species through the reduction in disturbance and/or fragmentation (13 cases each) and less frequently approaches for control (10 cases) or eradication of alien plants (nine cases).

Discussion

Globally, less than 13% of Earth's ice-free land falls under some form of legal protection (Jenkins & Joppa 2009) yet over 37% of impact studies are undertaken in protected areas, which suggests a significant bias. However, alien plant impact studies are less biased than other ecological studies that have been shown to situate over 60% of field sites in protected areas (Martin *et al.* 2012). We might expect an even stronger bias toward protected areas given the imperative to assess alien plant impacts where they are most likely to matter. That research on alien plant impacts is less biased toward protected areas than most ecological studies undoubtedly reflects the pervasive nature of biological invasions and the importance of their impacts on the wider function of seminatural ecosystems both within and outside of protected areas. Nevertheless, it indicates that compared to other pressures impacting upon protected areas, we may know relatively less about alien plant impacts.

The finding that the distribution of impact studies across biogeographic regions does not reflect the availability of protected areas in each region also suggests that alien plant impact studies are not strongly targeted toward protected areas. The Pacific islands have one of the lowest levels of protected area coverage (3%, Jenkins & Joppa 2009) yet over 60% of impact studies

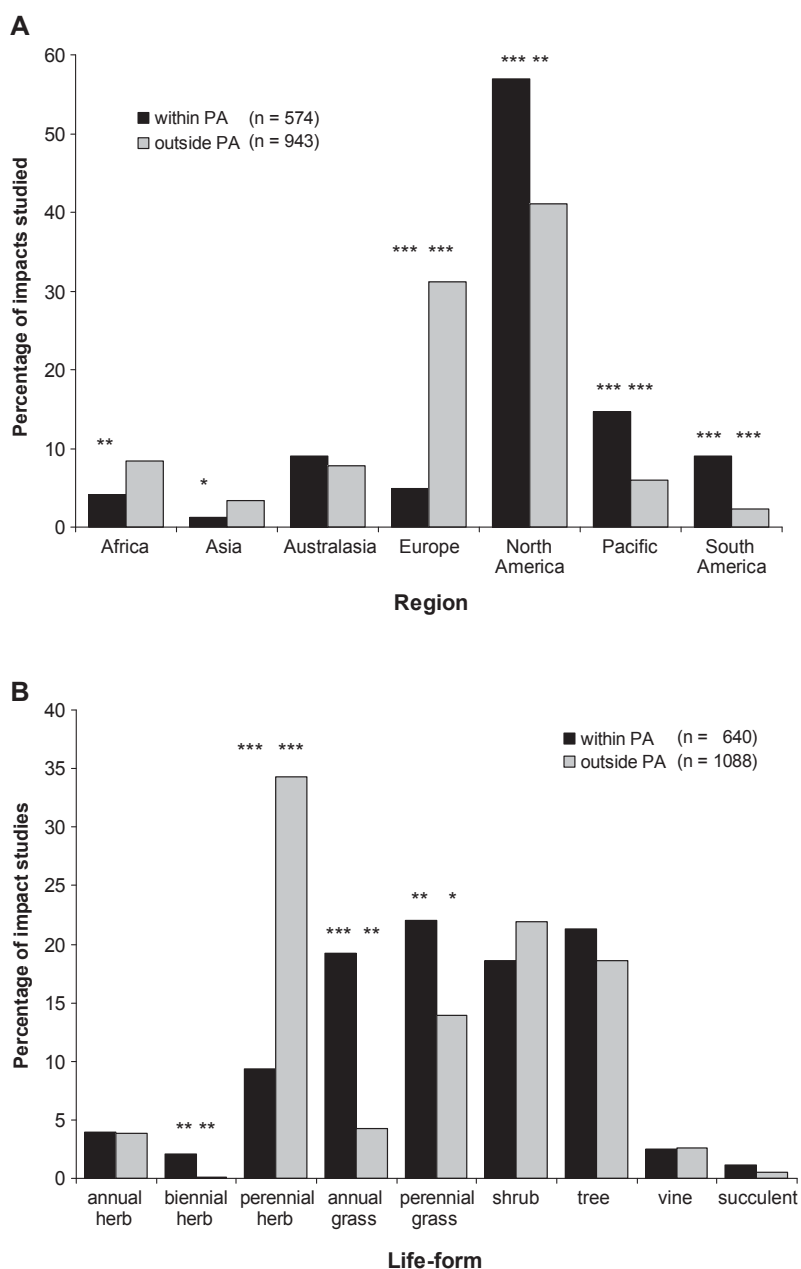


Figure 1 Frequency of impacts of alien plants addressed by studies conducted within and outside protected areas. Impacts classified according to (A) the geographic distribution of studies and (B) alien plant life-form. The percentage of impacts examined within and outside protected areas is shown separately for each category. Differences between observed and average frequencies were tested by a G-test on contingency tables. Categories with significantly fewer or more cases than expected by chance are marked: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Sample sizes for life-forms are greater than for regions since several species could be classed into more than one life-form (e.g., annual/biennial).

occur within these areas. In contrast, Europe has among the world's highest coverage (10–15%, Jenkins & Joppa 2009) yet only 9% of impact studies are in protected areas. The contrast between Europe and North America is striking. Although they have similar protected area coverage (10–15%, Jenkins & Joppa 2009), the proportion of impact studies undertaken within protected areas is five times greater in North America than Europe. One reason might be that the underlying level of invasion differs between these two continents. National parks in North America have a higher level of plant invasion, close to

30% (Allen *et al.* 2009) compared to only 6% found in European nature reserves (Pyšek *et al.* 2002). Thus, plant invasions may be more of a concern to the management of protected areas in North America and hence the subject of more research funding. The high frequency of impact studies found for Pacific island protected areas contrasts with the low coverage of protected areas in the Pacific region, suggesting quite specific targeting. Pacific islands are particularly vulnerable to plant invasions (Brockie *et al.* 1988; Lonsdale 1999; Kueffer *et al.* 2010) and thus perhaps the greater the threat of alien plants in protected

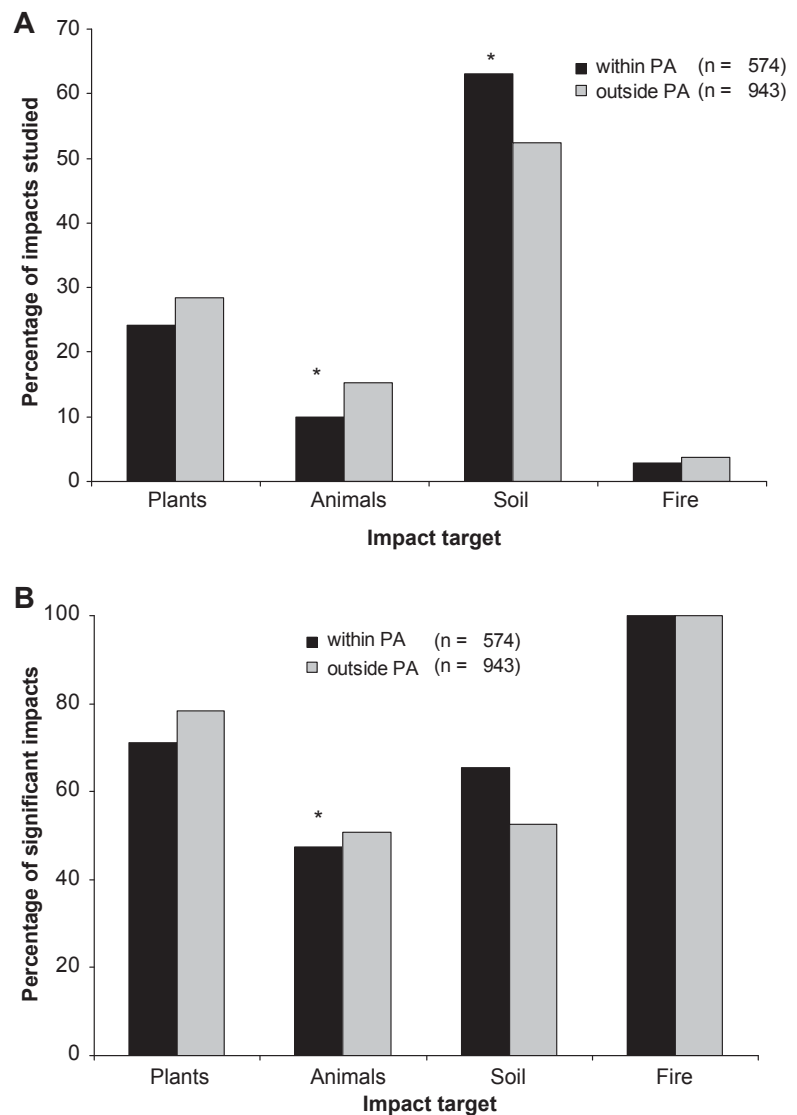


Figure 2 Trends within and outside protected areas in the extent to which (A) different impact targets have been studied and (B) the percentage of impacts that were found statistically significant (whether an increase or decrease in the response variable). Impacts were classified according to target into (i) populations, species, and communities of plants; (ii) populations, species, and communities of animals; (iii) soil characteristics; and (iv) fire regime. Differences between observed and average frequencies were tested by a G-test on contingency tables. Categories with significantly fewer or more cases than expected by chance are marked: * $P < 0.05$.

areas, the more likely impacts are to be studied. Given this research effort, we may expect better informed management of alien plants in protected areas in the Americas and Pacific but perhaps less so in other regions of the world. However, even with the increased attention to alien plant impacts in protected areas of Pacific islands, biodiversity in the region is dwindling and the protected area system remains inadequate (Keppel *et al.* 2012).

Quantitative studies addressing the impact of alien plants tend to be biased toward perennial herbs and grasses, as well as annual grasses when compared to a global compendium of invasive alien plant species (Hulme *et al.* 2013). This bias is even more marked in the differences in plant life-forms examined within and

outside protected areas with perennial and annual grasses also being more frequently examined within than outside protected areas. As a consequence, there is only limited evidence that alien plant species whose environmental impacts are of global concern are examined proportionally more in protected areas. This indicates that studies in protected areas are possibly not adequately addressing life-forms or species that might have major impacts on biodiversity and ecosystem function, such as vines and shrubs. The strong bias in North America toward annual grasses compared to the rest of the world undoubtedly reflects the considerable interest in one species in particular, *Bromus tectorum*. There is little overlap in the alien plant species examined within and outside protected areas, and thus the extent to which studies outside

protected areas can inform conservation priorities may be questionable.

Although differences in the frequency with which different responses have been examined are difficult to interpret given the biogeographic and species biases present in studies on impact, it may be indicative that studies in protected areas may only examine alien plant impacts on subcomponents of biodiversity and ecosystem function. A more holistic approach may be essential when prioritizing management or restoration efforts (Hulme *et al.* 2013). The lack of any difference within and outside protected areas in the proportion of significant impacts is of little comfort, given that in both cases, significant impacts are found more often than not for several response classes.

Although alien plant impacts are being quantitatively examined in protected areas, this is less than we might expect given the strong focus of ecological studies in these regions. How then should we address the study and management of alien plant impacts in protected areas? First, impact studies should provide managers with the necessary information to identify management priorities. Initial surveys of the level of plant invasion in protected areas may be valuable for prioritization but not if these are drawn, as they often are, from assessments in anthropogenic areas such as along roadsides (Pauchard & Alaback 2004; Wu *et al.* 2009). Of greater value are surveys that quantify the distribution and local abundance of alien plants within the natural ecosystems in protected areas. Such assessments can often be logistically challenging but may be cost-effective where integration with remote sensing data is possible (Gil *et al.* 2013).

Second, in the absence of other data, quantitative assessments of alien plant impacts should target the most widespread and abundant taxa. Few quantitative impact studies provide information on the distribution or abundance of the target alien plant species in the ecosystem concerned, or confirm that the abundance at which the species has been studied is representative of its wider distribution. Examining impacts across a representative range of alien plant abundances can identify key thresholds for ecosystem change (Hulme *et al.* 2013) and when linked to distribution data can assist with targeting management where it will be most effective.

Third, quantitative studies should examine biodiversity and ecosystem impacts that are of concern to securing the integrity and value of a protected area. Direct or indirect threats to one or more endangered species as a result of plant invasion may be perceived as of more concern than statistically significant changes in soil pH, cation concentration, or microbial richness unless the wider consequences of these more subtle impacts are addressed. Furthermore, there may be composite impact in-

dicators (e.g., changes in the functional richness of native plant communities) that may more rapidly inform of potential wider ecosystem effects of plant invasions. Better linkages between what impacts are measured and conservation outcomes are needed. Unfortunately, the evidence for the extent to which these studies are designed to inform management by targeting endangered species or restoration programs is weak. Only one-third of studies interpret their findings in terms of their implications for management of alien plants and even when this is undertaken, it is unclear whether the assessment of impacts was designed to inform future mitigation strategies.

Can more be done? Clearly, there is still considerable potential for a greater proportion of quantitative studies to be undertaken in protected areas. Future research must consider the implications of alien plant impacts in protected areas. In particular, research should identify whether impacts are themselves drivers of ecosystem change or primarily symptoms of wider environmental degradation, assess the reversibility of any impacts, and inform options for mitigation or control. In addition, better evidence-based information sharing regarding the impacts that specific alien plant species pose to particular protected areas would help inform management in locations that have no local quantitative evidence. Linking the World Database on Protected Areas (www.wdpa.org) and the Global Invasive Species Database (www.issg.org/database/welcome) would provide a mechanism to facilitate identification of plant species with known impacts in protected areas as well as share information on best management practices. As yet these two important global initiatives are not linked or easy to cross-reference. There therefore remains considerable scope to improve the evidence base on alien plant management in protected areas.

Acknowledgments

PP and JP acknowledge the support from long-term research development project no. RVO 67985939 (Academy of Sciences of the Czech Republic), grant no. P504/11/1028 (Czech Science Foundation) and institutional resources of Ministry of Education, Youth and Sports of the Czech Republic. PP acknowledges the support by the Praemium Academiae award from the Academy of Sciences of the Czech Republic, MV by projects RIXFUTUR (CGL2009-7515), Consolidar-Ingenio MONTES (CSD2008-00040), and the Junta de Andalucía project RNM-4031. We thank Zuzana Sixtová for technical assistance. It is with deep sadness that we note the recent passing of our dear colleague Vojta Jarošík.

References

- Allen, J.A., Brown, C.S. & Stohlgren, T.J. (2009) Non-native plant invasions of United States national parks. *Biol. Invasions*, **11**, 2195–2207.
- Andam, K.S., Ferraro, P.J., Pfaff, A., Sanchez-Azofeifa, G.A. & Robalino, J.A. (2008) Measuring the effectiveness of protected area networks in reducing deforestation. *Proc. Natl. Acad. Sci. USA*, **105**, 16089–16094.
- Andreu, J., Vilà, M. & Hulme, P.E. (2009) An assessment of stakeholder perceptions and management of noxious alien plants in Spain. *Environ. Manage.*, **43**, 1244–1255.
- Brockie, R.E., Loope, L.L., Usher, M.B. & Hamann, O. (1988) Biological invasions of island nature reserves. *Biol. Conserv.*, **44**, 9–36.
- Bruner, A.G., Gullison, R.E., Rice, R.E. & da Fonseca, G.A.B. (2001) Effectiveness of parks in protecting tropical biodiversity. *Science*, **291**, 125–128.
- Cook, C.N., Hockings, M. & Carter, R.W. (2010) Conservation in the dark? The information used to support management decisions. *Front. Ecol. Environ.*, **8**, 181–186.
- Dudley, N. (2008) *Guidelines for applying protected area management categories*. IUCN Gland, Switzerland.
- Gil, A., Lobo, A., Abadi, M., Silva, L. & Calado, H. (2013) Mapping invasive woody plants in Azores protected areas by using very high-resolution multispectral imagery. *Eur. J. Remote Sens.*, **46**, 289–304.
- GISP (2007) *Invasive alien species and protected areas: a scoping report part I. Scoping the scale and nature of invasive alien species threats to protected areas, impediments to management and means to address those impediments*. Global Invasive Species Programme (GISP), Available online at www.gisp.org/publications/reports/IAS.ProtectedAreas_Scoping_I.pdf. Accessed March 10, 2013.
- Groves, R.H. (2002) The impacts of alien plants in Australia. Pages 11–24 in D. Pimentel, editor. *Biological invasions: economic and environmental costs of alien plant, animal, and microbe species*. CRC Press, Boca Raton.
- Hulme, P.E. (2012) Weed risk assessment: a way forward or a waste of time? *J. Appl. Ecol.*, **49**, 10–19.
- Hulme, P.E., Pyšek, P., Jarošík, V., Pergl, J., Schaffner, U. & Vilà, M. (2013) Bias and error in understanding plant invasion impacts. *Trends Ecol. Evol.*, **28**, 212–218.
- Hulme, P.E., Pyšek, P. & Winter, M. (2012) Biosecurity on thin ice in Antarctica. *Science*, **336**, 1101–1104.
- Jenkins, C.N. & Joppa, L. (2009) Expansion of the global terrestrial protected area system. *Biol. Conserv.*, **142**, 2166–2174.
- Joppa, L.N. & Pfaff, A. (2011) Global protected area impacts. *Proc. R. Soc. B Biol. Sci.*, **278**, 1633–1638.
- Keppel, G., Morrison, C., Watling, D., Tuiwawa, M.V. & Rounds, I.A. (2012) Conservation in tropical Pacific Island countries: why most current approaches are failing. *Conserv. Lett.*, **5**, 256–265.
- Kueffer, C., Daehler, C.C., Torres-Santana, C.W., *et al.* (2010) A global comparison of plant invasions on oceanic islands. *Perspect. Plant Ecol. Evol. Syst.*, **12**, 145–161.
- Laurance, W.F. (2013) Does research help to safeguard protected areas? *Trends Ecol. Evol.*, **28**, 261–266.
- Leroux, S.J. & Kerr, J.T. (2013) Land development in and around protected areas at the wilderness frontier. *Conserv. Biol.*, **27**, 166–176.
- Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.
- Loope, L.L., Sanchez, P.G., Tarr, P.W., Loope, W.L. & Anderson, R.L. (1988) Biological invasions of arid land nature reserves. *Biol. Conserv.*, **44**, 95–118.
- Macdonald, I.A.W. & Frame, G.W. (1988) The invasion of introduced species into nature reserves in tropical savannas and dry woodlands. *Biol. Conserv.*, **44**, 67–93.
- Macdonald, I.A.W., Graber, D.M., Debenedetti, S., Groves, R.H. & Fuentes, E.R. (1988) Introduced species in nature reserves in mediterranean-type climatic regions of the world. *Biol. Conserv.*, **44**, 37–66.
- Martin, L.J., Blossey, B. & Ellis, E. (2012) Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations. *Front. Ecol. Environ.*, **10**, 195–201.
- Pauchard, A. & Alaback, P.B. (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. *Conserv. Biol.*, **18**, 238–248.
- Pickering, C. & Mount, A. (2010) Do tourists disperse weed seed? A global review of unintentional human-mediated terrestrial seed dispersal on clothing, vehicles and horses. *J. Sustain. Tour.*, **18**, 239–256.
- Pyšek, P., Jarošík, V., Hulme, P.E., *et al.* (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biol.*, **18**, 1725–1737.
- Pyšek, P., Jarošík, V. & Kučera, T. (2002) Patterns of invasion in temperate nature reserves. *Biol. Conserv.*, **104**, 13–24.
- Pyšek, P., Jarošík, V. & Kučera, T. (2003) Inclusion of native and alien species in temperate nature reserves: an historical study from Central Europe. *Conserv. Biol.*, **17**, 1414–1424.
- Radeloff, V.C., Stewart, S.I., Hawbaker, T.J., *et al.* (2010) Housing growth in and near United States protected areas limits their conservation value. *Proc. Natl. Acad. Sci. USA*, **107**, 940–945.
- Rose, M. & Hermanutz, L. (2004) Are boreal ecosystems susceptible to alien plant invasion? Evidence from protected areas. *Oecologia*, **139**, 467–477.
- Sodhi, N.S., Koh, L.P., Clements, R., *et al.* (2010) Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biol. Conserv.*, **143**, 2375–2384.
- Spear, D., Foxcroft, L.C., Bezuidenhout, H. & McGeoch, M.A. (2013) Human population density explains alien species

- richness in protected areas. *Biol. Conserv.*, **159**, 137-147.
- Timmins, S.M. & Williams, P.A. (1991) Weed numbers in New Zealand forest and scrub reserves. *New Zealand J. Ecol.*, **15**, 153-162.
- Usher, M.B. (1988) Biological invasions of nature reserves – a search for generalizations. *Biol. Conserv.*, **44**, 119-135.
- Vilà, M., Espinar, J.L., Hejda, M., et al. (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.*, **14**, 702-708.
- Weber, E. (2003) *Invasive plant species of the world: a reference guide to environmental weeds*. CABI Publishing, Wallingford.
- Williams, P.A. & Timmins, S.M. (2002) Economic impacts of weeds in New Zealand. Pages 175-184 in D. Pimentel, editor. *Biological invasions: economic and environmental costs of alien plant, animal, and microbe species*. CRC Press, Boca Raton.
- Wu, S.H., Tsai, J.K., Sun, H.T., Chen, C.F. & Chiou, C.R. (2009) Patterns of plant invasions in the preserves and recreation areas of Shei-Pa National Park in Taiwan. *Bot. Stud.*, **50**, 217-227.